# Interactive effects of ozone and climate on water use, soil moisture content and streamflow in a southern Appalachian forest in the USA

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## Summary

- Documentation of the degree and direction of effects of ozone on transpiration of canopies of mature forest trees is critically needed to model ozone effects on forest water use and growth in a warmer future climate.
- Patterns of sap flow in stems and soil moisture in the rooting zones of mature trees, coupled with late-season streamflow in three forested watersheds in east Tennessee, USA, were analyzed to determine relative influences of ozone and other climatic variables on canopy physiology and streamflow patterns.
- Statistically significant increases in whole-tree canopy conductance, depletion of soil moisture in the rooting zone, and reduced late-season streamflow in forested watersheds were detected in response to increasing ambient ozone levels.
- Short-term changes in canopy water use and empirically modeled streamflow patterns over a 23-yr observation period suggest that current ambient ozone exposures may exacerbate the frequency and level of negative effects of drought on forest growth and stream health.

**Key words:** Appalachia, climate, forests, ozone, soils, streamflow, water use.

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## Introduction

Among the predicted consequences of continued increases in greenhouse-gas emissions are increases in average global surface temperatures of 1.0–3.5 C by the end of this century (Kattenberg *et al.*, 1996). Responses of precipitation patterns to this global warming are less certain, and may include either increased or decreased annual rainfall and/or changes in seasonal rainfall distribution patterns (Schneider, 1989). The combination of a warming climate and at least episodic decreases in precipitation suggests that drought will become increasingly important in a warmer climate (IPCC, 2001). Chronic and episodic droughts that affect soil water availability mediate plant–soil and plant–plant interactions on a worldwide basis (Schulze *et al.*, 1987), and potential changes in drought frequency and/or severity have been considered a key scenario in evaluating the ecological consequences of future climate change (Wigley *et al.*, 1984). Such effects are anticipated to occur primarily through reduction in net primary productivity, differential effects among tree species and size classes, and increases in sensitivity of forests to insects, disease, and fire frequency with increases in drought (Hanson & Weltzin, 2000).

While increasing temperatures and reduced rainfall will reduce water availability for tree use, they are not the only components of climate change that will probably affect forest water balance. There is abundant evidence that tropospheric ozone ($O_3$), which, like emissions of greenhouse gases, is a byproduct of fossil fuel combustion, can alter trees' capacity to control water loss through stomata and hence their potential sensitivity to drought (Maier-Maercker, 1998; Mansfield, 1998). Stomatal responses to ozone are clearly complex, with variations in degree and direction of response being associated

with species, exposure concentration and length of exposure (McAinish *et al.*, 2002). There is some evidence that high ozone levels can cause stomatal closure and help protect plants from water loss (Tingey & Hogsett, 1985). However, many studies with seedlings and saplings in controlled exposures (Keller & Hasler, 1984; Reich & Lassoie, 1984; Skarby *et al.*, 1987; Lee *et al.*, 1990; Wallin & Skarby, 1992; Pearson & Mansfield, 1993; Matyssek *et al.*, 1995) indicate that, at near-ambient ozone levels, stomatal control of water loss may be reduced, with stomata responding sluggishly to environmental stimuli including delayed stomatal closure at night.

Because of the difficulties in scaling physiological measurements from seedlings to larger trees (Samuelson & Kelly, 2001), such observations of changes in stomatal function in response to ozone exposure suggest the need to determine how leaf-level responses are integrated at the level of whole forest canopies to influence tree- and stand-level water use. Empirical evidence from larger trees, including both *in situ* physiological measurements of foliage (Maier-Maercker & Koch, 1992; Maier-Maercker, 1997; Grulke *et al.*, 2002a) and tree- and stand-level growth responses (Zahner *et al.*, 1989; McLaughlin & Downing, 1995, 1996; Peterson *et al.*, 1995) in natural settings, suggests that drought effects may be enhanced, not reduced by concurrent stresses posed by ozone and reduced water availability. However, no studies have yet documented the nature and extent of effects of ozone at whole-tree and watershed scales, at ozone levels that currently occur across large regions of the industrialized world. Such information must be addressed appropriately in forest ecosystem models designed to predict the combined effects of climate change on forest growth and ecosystem function.

In a related study (McLaughlin *et al.*, 2007), we detected statistically significant effects of ambient ozone levels in East Tennessee on tree growth and water use. We concluded that seasonal growth cycles were affected at least partly through ozone effects on water-loss rates. This was evidenced by ozone–induced increases in average sap-flow rates over the growing season. These results further led us to hypothesize that canopy-level responses would be detectable at a watershed scale in our study region. In particular, we examined baseflow, a hydrological term that describes the background flow rates associated with slower drainage from watershed soil/aquifer systems. Baseflow levels are attained after subsidence of the overland and shallow surface flows that follow significant storm events. Forest hydrologic research around the world suggests that changes in forest cover affect streamflow mostly through altering the baseflow component during the growing seasons (Chang, 2003). For the Appalachian region, streamflow is typically reduced to near-baseflow levels during much of August, September and October. During this time, flows are typically reduced by low precipitation inputs and are sustained by shallow groundwater reserves linked to soil moisture in the unsaturated zone (Hewlett, 1982). As soil moisture is depleted, baseflow is reduced to minimum values (Smakhtin, 2001). Over 70% of the streamflow in forested watersheds in our study region is contributed by baseflow, on an annual basis. This percentage is even higher in the dry seasons (Hewlett, 1982) and late in the growing season, when flows are typically low because of drier conditions. Under these conditions, forest water use plays a relatively more important role in streamflow patterns. Baseflow rates are very important to stream ecology, but much related hydrologic research has been done in order to understand historical low-flow periods (Giese & Mason, 1991; Evett *et al.*, 1994), rather than the causal effects of variations over time. Soils, climate, and both the amount and physiological activity (transpiration rate) of vegetative cover are known to influence baseflows (Andreassian, 2004). To our knowledge, no forest hydrologic literature has examined ozone effects on baseflow at the watershed scale.

The objectives of this study were to define potentially significant interactions among background ozone levels, climate, and forest water use. This involved initial studies at a whole-tree level at a single site. The purpose was to quantify interactions between ozone and climate variables that could change water use by individual trees at an hourly to daily scale. These were followed by analysis of the potential significance of those types of change at a watershed scale using monthly flow rates across annual time steps. These measurements involved three forested watersheds, which varied in size from 97 to 28 000 ha. In these studies, changes in annual baseflow levels were measured in response to annual variations in ozone and traditional environmental variables known to influence streamflow.

## Materials and Methods

### Experimental design

These experiments were part of a larger study designed to characterize variations in tree growth and tree water use in response to natural variations in ozone and meteorological variables, at diverse forested sites in eastern Tennessee, USA. In a related study (McLaughlin *et al.*, 2007) we reported changes in growth and whole-tree water use observed at the most intensively measured site at Look Rock, TN. Those measurements indicated that peak hourly ozone exposures stimulated whole-tree water used as measured by stem sap flow (Granier, 1987). These responses then resulted in reduced stem expansion and seasonal growth. Here we examine the implications of changes in water use in terms of altered canopy conductance, changes in soil moisture in the rooting zone of measured trees, and evidence that these types of response could be detected over longer periods at the watershed scale through measures of altered stream-flow patterns.

Measurements of sap flux and soil-moisture status were made at Look Rock, TN, a ridgetop site at 800 m elevation located along the Foothills Parkway, approx. 15 km south-east of the Great Smoky Mountains. Measurements were restricted to six trees, a number limited by solar power supply

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capacity at this remote site. The six sensors were distributed among the 14 available trees accessible with the wired stem increment-monitoring system (McLaughlin *et al.*, 2007). The sapflow sampling included triplicate samples of red oak (*Quercus rubra* L.), an intensively monitored species, with one each apportioned to species with diverse ecological attributes. These included pitch pine (*Pinus rigida* Mill.), hickory (*Carya* sp.), and yellow poplar (*Liriodendron tulipifera* L.). Environmental data for the site, including radiation, temperature, precipitation, relative humidity and ozone-exposure concentrations, were obtained from a continuous-monitoring site maintained by the National Park Service within 1 km of the study site. A summary of types and sources of environmental data for 2001 and 2002 at the Look Rock Site is provided in Table 1.

**Table 1** Environmental contrasts in 2001 and 2002 at the Look Rock (TN, USA) site

| Variable | DOY | 2001 | 2002 |
|---|---|---|---|
| Rainfall (mm $h^{-1}$) | 121–180 | 0.14 | 0.16 |
| | 181–228 | 0.22 | 0.17 |
| Temperature ( C) | 121–180 | 18.6 | 18.8 |
| | 181–228 | 21.9 | 23.4 |
| Vapor-pressure deficit | 121–180 | 0.85 | 0.78 |
| ($g_{water}^{-1}$ $g_{dry\ air}^{-1}$) | 181–228 | 0.81 | 0.98 |
| Radiation (W $m^{-2}$ $h^{-1}$) | 121–180 | 218 | 229 |
| | 181–228 | 206 | 227 |
| $O_3$ AOT60 (ppm h) | 121–180 | 5.2 | 7.4 |
| | 121–228 | 7.7 | 18.5 |
| | 91–304 | 11.5 | 24 |
| $O_3$ max *H* $d^{-1}$ (ppb) | 121–180 | 68.1 | 69.2 |
| | 181–228 | 64.9 | 82.9 |
| Palmer Drought Severity | 121–180 | 0.12 | –0.88 |
| Index (PDSI)* | 181–240 | 1.12 | –1.54 |
| | 91–240 | 0.23 | –0.54 |
| 1982–2004: | | | |
| Historical PDSI | Average | Max. | Min. |
| (DOY 91–240) | 0.47 | 4.56 | –4.37 |

Averaged data are presented; the growing season has been divided into time periods before and after June 30 (DOY180): Data on temperature, radiation, rainfall and ozone concentrations at the Look Rock site were obtained from a National Park Service monitoring site at Look Rock, approx. 500 m from the study site (http://www2.nature.nps.gov/air/data/index.htm).
*PDSI measures cumulative meteorological drought derived from measures of moisture supply in rainfall, moisture storage in representative soils of the region, and drying potential of the atmosphere (Palmer, 1965). The PDSI scale of relative drought severity ranges from ≤ –4.00 (extreme drought) to ≥ +4.00 (extremely moist). Values in the range –1.99 to +1.99 are considered mid-range. Moderate values of moisture (+) or drought (–) are ±(2.00 to 2.99) and severe are ±(3.00 to 3.99). Data used in these studies were obtained for east Tennessee from the National Oceanic and Atmospheric Adminstration, National Climate Data Center (http://www.ncdc.noaa.gov/oa/climate/research/prelim/drought/palmer.html).

**Measurements of whole-tree water use** Six trees were selected for hourly measurements of sap flux in 2001 and 2002. Species included red oak, yellow poplar, hickory and pitch pine. These trees were largely canopy dominants or codominants based on height and crown area. Diameter at breast height ranged from 27.7 to 45.2 cm. The objective of these measurements was to describe patterns of sap flow observed in response to environmental stimuli, not to define the stomatal mechanisms involved. Instantaneous xylem sap flux was measured with 30-mm continuously heated thermal dissipation probes (TDP-30, Dynamax, Houston, TX, USA). Additional measurement details are given in the Supplementary Material (Section S1).

To evaluate the relationship of changes in sapflow to changes in whole-tree canopy conductance of water to the atmosphere, measurements of sap flux were normalized by dividing average daily sap flux by the daily 12-h maximum vapor-pressure deficit (VPD). This provided a generalized indicator of whole-canopy conductance according to the Ohms law analogy $E = IR$, where $E$ is gradient potential, $I$ is current flow rate, and $R$ is resistance, the inverse of conductance ($1/R$). Thus:

canopy conductance = sap flow/VPD

The units of these calculations, as scaled for graphical presentation, were $mm_{sap\ flow}\ s^{-1}\ (g_{water\ deficit})^{-1} \times 50$. While more precise calculations that partition pathway resistances into their individual components are typically used in calculating conductance of individual leaves, we consider the generalized whole-tree canopy-level conductance computed here to be appropriate for this context.

**Soil-moisture probe installation and calibration** The soil-moisture probes used in this study were Model CS615 ceramic probes produced by Campbell Scientific Inc (Logan, UT, USA). These probes were distributed at depths of 10 and at 22.5 cm, primarily near stem bases of trees for which sap flow was measured. They measured moisture-induced changes in temperature conductance following periodic pulse heating from a solar-charged marine battery system. They were calibrated against a subset of colocated time domain reflectometry soil-moisture probes that were measured manually at approximately biweekly intervals. Calibrations were done for probes buried at 10 and 22.5 cm at a distance of 1 m from the base of selected trees during the 2001 growing season.

## Streamflow data acquisition

The nature of responses to ozone of sap flow and soil moisture became apparent during the course of the study, suggesting that tree-level increases in water use might be detectable over time in observed streamflow patterns of local and regional watersheds. Preliminary short-term analyses from the Little River watershed near Look Rock supported this possibility. Ultimately, streamflow data were obtained from gauging

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stations at all three monitored forested watersheds within a 75-km radius of the study sites, to evaluate potential ozone effects on forest water use at larger scales. The watersheds were within the same air sheds and climatic divisions, and were forested with mixed deciduous forest cover similar to the growth-study plots. Historical streamflow and environmental data were obtained from Walker Branch Watershed (WBWS), a 94-ha long-term research watershed at Oak Ridge National Laboratory (P. Mulholland, pers. comm.) and from two nearby US Geological Survey streamflow-gauging stations (http://waterdata.usgs.gov/nwis/discharge). They included Cataloochie Creek, NC, which drained a 12 500-ha watershed in the north-eastern corner of the Great Smoky Mountains, and a station near Townsend, TN, on the Little River, which drains 28 000 ha of the western Smoky Mountains. Sources of additional monitoring data for watershed analysis are provided in Supplementary Material Section S2. Stepwise multiple regression, including analyses of best regression subsets at varying levels of model complexity of daily sap flow/canopy conductance and soil moisture and daily and monthly streamflow data were used to consider the individual and combined effects of a wide range of environmental variables on tree, soil and watershed responses.

## Data-analysis strategies

Because environmental data such as temperature, radiation and ozone are often interrelated in both their temporal patterns and their biological effects, it was important in our analyses both to address an appropriate range of environmental variables that could influence the dependent variables examined at each scale (tree water use, soil-moisture status, streamflow), and to match appropriate timescales for relating responses to predictor variables at each organizational level. Thus we conducted exploratory analyses (Statistix, 2000) with a wide range of predictor variables and averaging intervals, to define appropriate variables to be considered in multivariate models designed to predict daily patterns of tree water use and soil-moisture status, and annual patterns of streamflow. To explore cross-correlations among candidate independent variables and the biologically based dependent responses, we have computed correlation coefficients to define the magnitude of cross-correlations among all variables for which significant responses were detected. We have also calculated partial correlations for these variables to isolate their effects from those of other predictor variables. Only variables that were identified as statistically significant (typically at $P \leq 0.05$) were included in final models developed at each analytical scale, and these also are identified. The functional identities of all variables examined in each of the three classes of empirical model developed (canopy conductance, soil moisture, streamflow), and both cross-correlations and serial correlations for these variables, are presented in Supplementary Material ( Tables S1–S3 in Section S2).

**Modeling daily canopy-conductance patterns** Sap flow data from which estimates of canopy conductance were derived were analyzed as daily averaged rates of water transport for each individual tree. We screened a wide variety of predictor variables and response times for both independent and dependent variables, and ultimately found that the 24-h average sap flow was the best dependent variable. It allowed us to capture effects on total daily water use, which would include any effects of a delay in stomatal closure. A comparison of maximum hourly, 6-h and 8-h average ozone concentrations identified the maximum hourly ozone concentration each day as most influential in affecting daily average sap flow and hence canopy conductance. We also examined a range of formulations of $O_3$, radiation, rainfall, temperature and VPD in order to explore the effects of average environmental conditions at times ranging from 1–3 d before the sap flow measurement day (Tables S1–S3). Ultimately, a stepwise regression model was run for each of the six trees with the potential predictor variables describing preceding temperature, rainfall, solar radiation, vapor pressure and ozone exposure (Table S1).

**Modeling soil moisture responses to ozone and other environmental variables** Because soil moisture responds more slowly to physical and biological variables that affect water availability, soil moisture modeling included both biological and physical variables and longer time averaging than for tree water use. These were decided based partly on variables selected as significant in previous sap-flow analyses. However, for soil moisture analyses, lag times were increased to up to 11 d preceding the measurement day, to include appropriate influences of both inputs (rainfall) and withdrawal (transpiration) by trees. The timeframes chosen were also guided by examining the time course of soil moisture draw-down following specific rainfall events during the growing season. The dependent variable used was soil-moisture status at 6 : 00 am on the measurement day (day 0). In general, average $O_3$, temperature and VPD levels during the 3 d before day 0 were found to influence soil-moisture status significantly on day 0. The influence of time-weighted rainfall for periods of up to 11 d before day 0 were sometime detectable, while comparably time-weighted sap flow, a measure of demand that was also significantly influenced by $O_3$, was often detectable for time-weighted periods including the 11 d preceding day 0.

**Modeling streamflow patterns** To test the potential relevance of relationships between climatic variables and water use identified in whole-tree studies, we examined historical streamflow patterns for three watersheds ranging in size from 97 to 28 000 ha. Our analyses focused on evaluating factors involved in influencing year-to-year variations in baseflow during low-flow periods (August–October), when the transpiration uses a significant fraction of the water available for drainage to receiving streams and interference from storm events is reduced.

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Differences in tree water use and soil-moisture status between 2001 and 2002 at the Look Rock site initially led us to look for simple empirical relationships in streamflow that might express those differences at a watershed scale. In our study region, the Little River near Townsend, TN, which drains 28 000 ha of the forested south-western slopes of the Great Smoky Mountains, provided an initial test of relationships of streamflow with apparent changes in forest water use. Comparisons of late-season flow for 2001 vs 2002 indicated that rather large differences in empirical indices of streamflow accompanied observed changes of indices of water use at the tree and soil levels noted at Look Rock. Compared with 2001, these included a 25% reduction in streamflow per unit of rainfall; a 55% reduction in streamflow in relation to VPD level; and a 66% reduction in streamflow in relation to sap flow in 2002. All these comparisons suggested a functional change in the water budget for Little River in 2002, the high-ozone year.

Further exploratory analyses were conducted using monthly data for a wide range of environmental variables that were identified as potentially useful in predicting monthly flow from August to October (Table 1). Finally, more intensive baseflow analyses were derived from daily streamflow hydrographs for the most complete data set from WBWS using the standard flow-separation technique described by Hewlett (1982). This method assumes that baseflow in a hydrograph increases at a rate of 0.033 mm $h^{-1}$ during a storm event from an initial baseflow condition. Streamflow higher that the calculated baseflow rate was classified as stormflow. Daily baseflow values were then summed up as monthly baseflows for monthly scale statistical analyses for this watershed.

## Results

### Changes in rates of water use by trees

The changes in the amplitude of daily and seasonal stem-increment patterns noted in another study suggested that, despite rather low stress indicated by the Palmer Drought Severity Index (PDSI; Table 1), sampled trees were episodically under greater water stress in 2002 than in 2001. An initial exploratory test of our working hypothesis that ozone would increase water use by forest trees is examined in Fig. 1. We found an almost linear increase in an average of daily sap flow for each of the three species across the full range of increasing daily $O_3$ exposure maxima ($O_3$MaxHD). Evidence of diminishing increases or declining sap flow with increasing ozone was restricted to only the highest 4% of all daily ozone values observed.

Increases in both VPD and ozone levels (Table 1) in 2002 were potential contributors to increased water use during that year. Stepwise multivariate modeling was subsequently used to consider the individual and combined contributions of candidate variables to observed changes in water-use rates. These empirical models were then used to explore the sensitivity of observed responses to systematic reduction in levels of $O_3$ either over the growing season (conductance and soil moisture) or across years (streamflow).

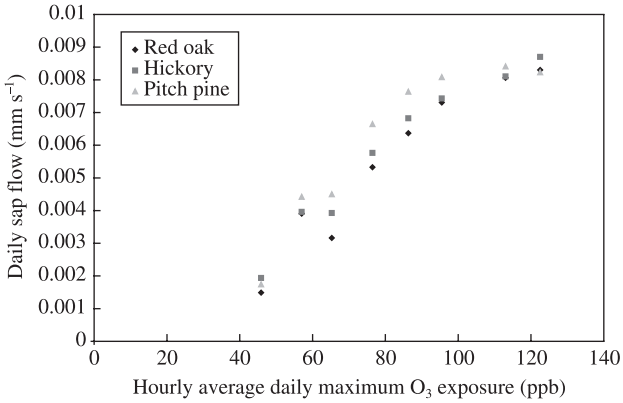


**Fig. 1** Average sap flow in response to increasing ozone concentrations for three individual trees representing three tree species at Look Rock, TN, USA in 2002.

**Modeling daily averaged canopy conductance and soil-moisture status** As VPD typically increases with increasing $O_3$, we developed stepwise multiple regressions to consider concurrent influences of these and other variables as predictors of daily water use by trees. Our previous analyses using stepwise regression analysis identified $O_3$ ($O_3$MaxHD), temperature and soil-moisture status as the most consistent and statistically significant variables affecting sap flow of the six trees examined in 2002. The influences of ozone were reduced and the influence of VPD increased during the preceding year, when $O_3$ levels were lower.

Because VPD levels were higher in 2002 than in 2001, we evaluated the specificity of the sap-flow response by normalizing sap flow (SF) to concurrent VPD levels in 2002, providing an indicator of variations in whole-tree canopy conductance. Daily changes in estimated whole-canopy conductance (SF/VPD) were used with the same independent variables used in sap-flow analyses to derive a stepwise multiple regression model. The model of estimated daily average canopy conductance for red oak 18 (RO18) in 2002, compared with measured daily SF/VPD (Fig. 2), took the form:

$$\begin{aligned}\text{canopy conductance} = &-0.051 + 0.0037(O_3\text{MaxHD}_{d0}) \\ &- 0.3997(\text{VPDmax12H}_{d0}) \\ &- 0.0924\ (\text{RO11SM10}_{d0}) \\ &+ 0.0207(\text{Temp-avg}_{d0}) \\ &+ 0.1900(\text{VPDmaxh}_{d0}) \\ &+ 0.1056(\text{Rain}_{d0})\end{aligned}$$

The model $R^2$ was 0.41 ($P < 0.05$ for $n = 110$). The effects of the maximum daily $O_3$ on daily average canopy conductance were highly significant ($P \leq 0.004$). Other significant variables were daily average temperature (Temp-avg$_{d0}$), soil moisture (SM at

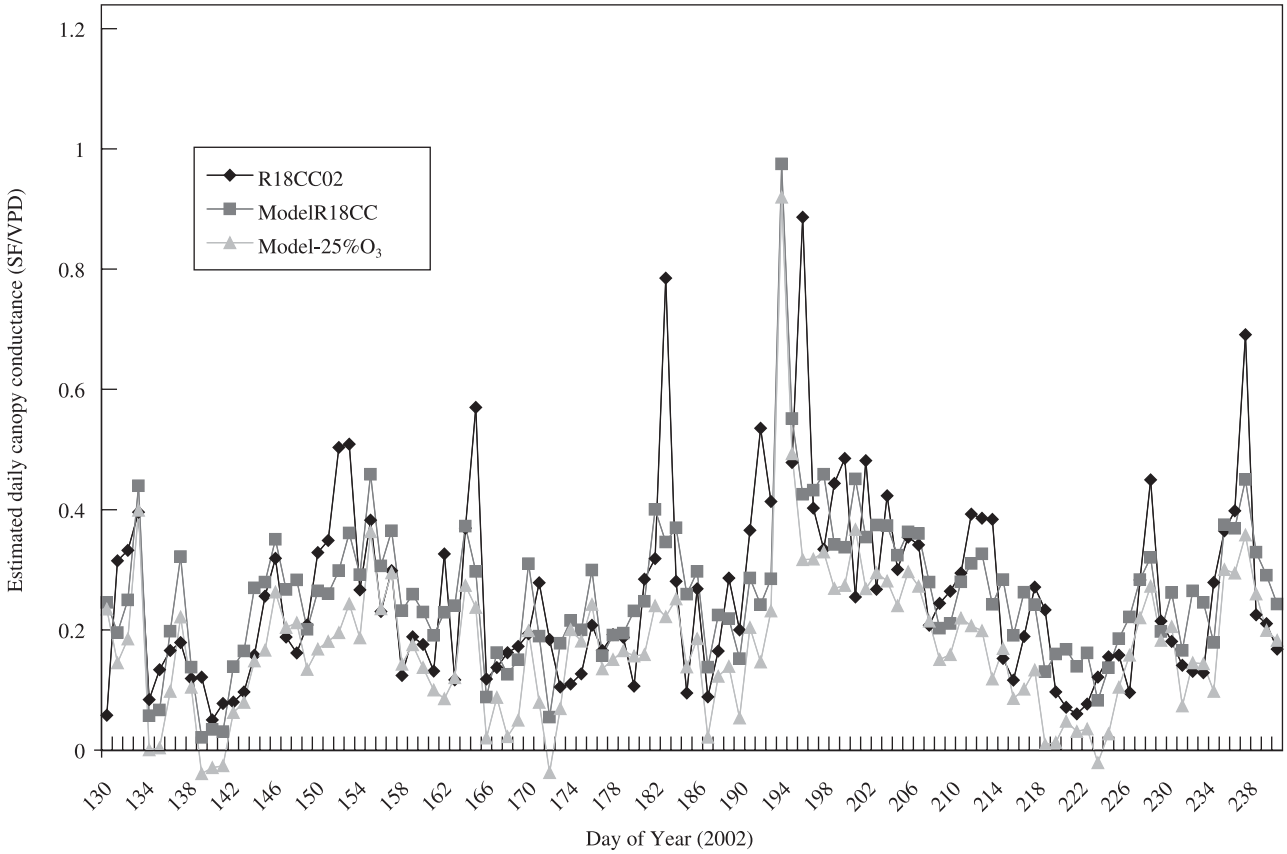


**Fig. 2** Actual and modeled estimates of whole-canopy conductance of Red Oak 18 during the 2002 growing season at Look Rock, TN, USA. Units of canopy conductance are $mm_{sap\ flow}\ s^{-1}\ (g_{water\ deficit}\ g_{dry\ air}{}^{-1})^{-1} \times 50$. Modeled conductance incorporated ambient levels of temperature, vapor-pressure deficit, rainfall and maximum hourly ozone exposure per day. An additional simulation with a 25% reduction in peak ozone levels is shown.

10 cm near red oak 11), and VPD expressed as maximum 12-h average ($VPDmax12_{d0}$) and the daily maximum hourly value ($VPDmaxh_{d0}$). Estimated seasonal canopy conductance of RO18 was 99.6% of actual averaged conductance, and the coefficient of variation (CV) was 60% for the model compared with 47% for measured values. As with sap flow, the sensitivity of the model to systematically reducing maximum daily ozone exposure ($O_3MaxHD_{d0}$) by 25% over the entire growing season was evaluated. Average canopy conductance was estimated to be reduced by 31% at these reduced $O_3$ levels, as shown in Fig. 2. Model structure and performance for each of the six trees monitored in 2002 are documented in Table S1.

**Modeling soil-moisture patterns** The effects of ozone in increasing tree water use were also detectable in the surface soils in proximity to the trees for which sap flow was measured. Estimated soil moisture (% volume) ranged from 7 to 22% at Look Rock in 2002. Analyses revealed increasing importance of $O_3$ exposure on soil water status in 2002, just as was found with canopy conductance. In 2001, preceding rainfall and VPD were the most significant influences on soil-moisture status, whereas VPD, water withdrawal (sap flow) and $O_3$ became increasingly important in 2002. The shifts in relative statistical significance of environmental variables affecting soil moisture are shown in Table 2.

**Table 2** Analyses of variables significantly affecting soil-moisture status measured within 1 m of subject trees*, showing increased importance of vapor-pressure deficit, ozone ($O_3$) and sap flow in 2002

| | Significant responses | | | |
|---|---|---|---|---|
| | 2001 (five probes) | | 2002 (10 probes) | |
| Variable | $P \leq 0.05$ | $P \leq 0.25$ | $P \leq 0.05$ | $P \leq 0.25$ |
| Rain | 5 | 0 | 0 | 7 |
| Temperature | 1 | 0 | 1 | 2 |
| Vapor-pressure deficit | 4 | 1 | 10 | 0 |
| $O_3$ | 0 | 0 | 5 | 5 |
| Sap flow | 3 | 0 | 10 | 0 |

*In 2001, three tree species (hickory, red oak and chestnut oak) were represented, with three probes at 10 cm and two at 22 cm. In 2002, three probes at 10 cm and seven at 22 cm were distributed among seven trees representing four species (hickory, red oak, chestnut oak and pitch pine).

The stepwise multiple regression models developed to describe responses of soil moisture within 1 m of subject trees

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typically identified maximum hourly ozone exposure during the previous day, and both VPD and temperature in the preceding 2–3 d, as significant influences on soil moisture availability. For model development, we have used the actual data that report relative soil dryness as measured by temperature-conductance time. Data on sap-flow rates of adjoining trees substantially improved the predictive power of these empirical models. For soil within 1 m of red oak 30 (RO30), for example, the model for soil-moisture status at a depth of 22 cm took the form:

$$\begin{aligned}\text{soil dryness} = &-0.03697 - 0.00968(\text{Arain}_{d1})\\ &- 0.0195(\text{Arain wt-avg}_{d1:3})\\ &+ 0.00811(\text{O}_3\text{MaxHD}_{\text{avgd1}:3})\\ &- 148(\text{SFH21wt-avg}_{d1:11})\\ &+ 79.28(\text{SFR18wt-avg}_{d1:11})\\ &+ 0.0839(\text{temp-avg}_{d1:3})\\ &+ 0.00588(\text{DOY})\end{aligned}$$

The model $R^2$ was 0.74 ($P < 0.04$, $n = 130$), and the $O_3$ term (maximum average hourly $O_3$ days 1 : 3 before d0) was significant at $P \leq 0.01$. Other significant variables included averages of rainfall (Arain), sap flow (SF; H21, hickory 21; R18, red oak 18) and temperature data from 1–11 d ($\text{avg}_{d1:11}$) before the measurement day (d0) as well as time (day of year, DOY). Estimated soil-moisture levels averaged 100% of measured levels with CV values for estimated and measured values being of 20 vs 23%, respectively, over the 2002 growing season. Model simulations at daily ambient and ambient minus 25% $O_3$ exposure are shown in relationship to monitored values of soil moisture (soil dryness) in Fig. 3. Similar empirical models developed around other soil probes at Look Rock in 2002 are documented in Table S2.

Comparisons of the PDSI for 2002 with longer-term averages for east Tennessee (Table 1) indicate that 2002 was within the mid-range of PDSI values for this region. Based on the empirically derived dryness : moisture calibration curve for Look Rock soils, the increase in calculated soil moisture (volumetric percentage) resulting from model simulations of a 25% reduction of daily maximum ozone-exposure levels would be approx. 7% (Fig. 3). An increase of this magnitude would represent approx. 40% of the moisture available for plant uptake at average soil moisture levels in 2002. Thus a 25% reduction in peak ozone exposures would probably have benefited tree growth significantly under these conditions.

## Changes in historical streamflow patterns

Our analyses of streamflow patterns included the three nearest instrumented forested watersheds in proximity to our test plots within the region. These included two streams, Little River and Walker Branch, that were within 5 km of the forest test plots at Look Rock and Oak Ridge, respectively. The third

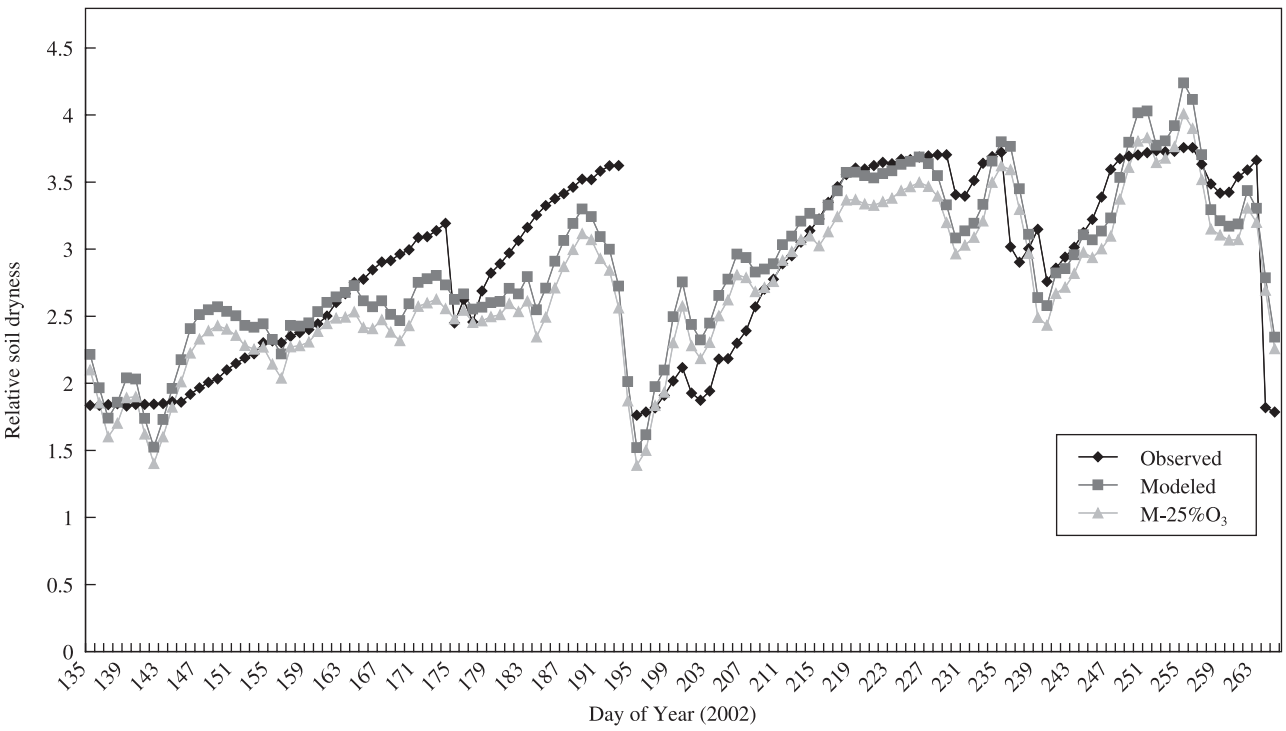


**Fig. 3** Actual and modeled soil moisture (dryness) at 22.5-cm depth near Red Oak 30 during the 2002 growing season. Soil water was estimated to range from a minimum of 7% (v/v) at maximum soil-probe values (3.75) to a maximum of 22% of soil volume at minimum soil-probe values (1.75; Table S1 in Supplementary Material Section S2). Modeled soil moisture considered ambient daily temperature, rainfall, sap flow of adjoining trees, time, ozone exposure, and a scenario with ozone reduced by 25% over the entire season.

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was Cataloochie Creek, which drained the north-eastern slopes of the Great Smoky Mountains, approx. 12 km from the Twin Creeks plot. We have included the results of empirical models derived from exploratory analyses using monthly averaged data for all three watersheds in Table S3, as well as more detailed analyses using classical hydrologic techniques and daily data. These analyses were restricted to the smallest watershed, Walker Branch, which had the longest period of record (23 yr) for both flow and environmental data. Watershed-level responses observed in preliminary analyses of monthly averaged data were as follows.

**Little River near Townsend** There were only 7 yr continuous data for this 358 $km^2$ watershed, so the empirically derived regression model, while statistically significant, could not be considered robust. However, cumulative $O_3$ exposure at or above 60 ppb (sumO60) was the strongest variable for the growing season when combined with temperature and precipitation variables, including a calculated cumulative VPD variable constructed to mirror the formulation of cumulative $O_3$ exposure. A simple regression model with cumulative $O_3$, included with strongest temperature and precipitation variables, had an $R^2$ of 0.75. The effect of $O_3$ on baseflow was identified as statistically significant ($P \leq 0.001$).

**Cataloochie Creek, NC** This 12 500 ha forested watershed draining north-east slopes of the Great Smoky Mountains National Park had continuous streamflow data for 22 yr (1982–2003), but $O_3$ data were available for only 15 yr. The exploratory regression model for average streamflow (August–October) was highly significant ($P < 0.01$, $n = 15$) with $R^2 = 0.75$, and included terms for both cumulative ozone exposure (sumO60) and PDSI. Ozone exposure was significant at $P < 0.01$.

**Walker Branch Watershed** WBWS is a long-term research watershed maintained on the US Department of Energy Oak Ridge National Environmental Research Park, by the Oak Ridge National Laboratory. The watershed is forested and comprises two branches with a total area of approx. 95 ha. Data from the east and west branches were combined for this study.

Initial analyses at this lower-elevation watershed (Table S3) were conducted using monthly averaged data. The exploratory stepwise regression model based on monthly data identified significant $O_3$ effects only for October flow. Predictor environmental variables included two ozone terms: AOT60 and MaxHD. Accumulation over Threshold 60 ppb (AOT60) summarizes ozone exposure hours that exceed 60 ppb. $O_3$MaxHD is the maximum hourly ozone exposure concentration per day. This value was averaged for the growing season and parts thereof for streamflow analyses. The model also included average PDSI and precipitation for August–October. Model $R^2$ was 0.85 ($P < 0.02$ with $n = 22$), and both $O_3$ terms were also highly significant ($P \leq 0.001$).

More refined analyses of the WBWS data set, which involved initial analyses conducted at a daily scale and then integrated to the monthly scale, identified significant ozone effects on the averaged flow over the entire low-flow interval (August–October). Correlations between late-season baseflow during the August–October period and a wide range of candidate predictor variables (Table S3) were examined. Regression analysis indicated that averaged baseflow during August–October correlated well with a suite of four environmental variables. These included averaged precipitation over the August–October interval, PDSI averaged for April–October ($PDSI_{4:10}$), and two descriptors of high $O_3$ exposures. The model took the form:

$$\begin{aligned}\text{August–October baseflow} = {} & 51.64 + 0.100(ppt_{8:10}) \\ & - 0.864(O_3MaxHDM_{avg4:10}) \\ & + 1.268(AOT60sum_{4:10}) \\ & + 1.532(PDSIavg_{4:10})\end{aligned}$$

Comparisons of actual and modeled late-season baseflow for WBWS over the interval 1982–2004 (Fig. 4) indicated relatively high predictive powers ($R^2 = 0.75$, $P < 0.005$) of the empirically derived multivariate regression model. The statistical significance of included terms was as follows: $O_3$MaxHDM averaged for April–October ($avg_{4:10}$, $P \leq 0.004$); precipitation, $ppt_{8:10}$ ($P \leq 0.088$); $PDSI_{4:10}$ ($P \leq 0.114$); and accumulative $O_3$ exposure (> 60 ppb), $AOT60_{4:10}$ ($P \leq 0.238$). Predicted baseflow over the 23-yr period averaged 99% of measured baseflow with CV values of 31 and 36%, respectively. Systematic reduction of maximum daily ozone levels by 25% across years resulted in an average increase in simulated baseflow by 62% for the August–October interval. This compares with an observed range in variability of annual baseflow (maximum : minimum percentage) of 350% for this watershed over the 1982–2004 study interval. It is important to note that, while baseflow during the relatively drier August–October interval comprised approx. 95% of total streamflow during that time, baseflow during the August–October interval averaged only approx. 8.5% of total annual flow for this site over the 23-yr study interval. Thus a 25% reduction in $O_3$ exposure and associated 62% increase in August–October baseflow, as estimated in Fig. 4, was projected to increase total longer-term average annual streamflow by only approx. 5%. This effect would be larger if increased water use by trees occurred over the whole growing season, as inferred by canopy-conductance analyses (Fig. 2). We did not evaluate potential changes in streamflow over the entire growing season in the present study.

## Discussion

### Implications of changes in whole-tree water use

Enhancement of the amplitude of the daily water-loss and recovery cycles observed in the present study following highest

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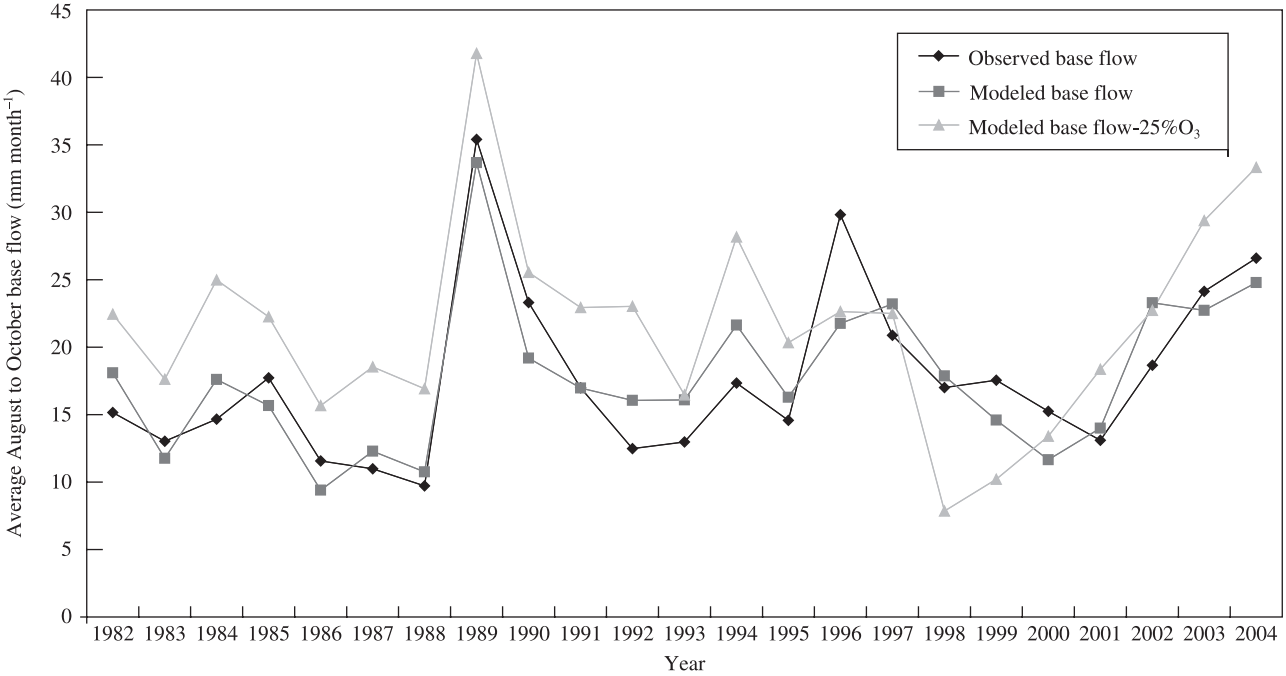


**Fig. 4** Measured and modeled baseflow of Walker Branch Watershed over 23 yr. The empirical model was based on annual precipitation, Palmer Drought Severity Index and ozone exposure, and included a scenario in which ozone levels were reduced by 25%.

ozone exposures suggest an ozone-induced interference in whole-tree water balance. Such patterns would probably result from ozone-induced increases in daytime transpiration. Potential enhancement of daily drought cycles by ozone exposure has been reported for foliage of Norway spruce trees, and was attributed to reduced stomatal control of water loss (Maier-Maercker, 1997). Increased stomatal aperture, altered stomatal responsiveness to environmental control, and reduced stomatal closure at night are potential contributors to increased total water-loss rates. Increased nighttime stomatal conductance in response to increasing ozone levels has been found to range from 10–20% of daytime values in mature ponderosa pine (Grulke *et al.*, 2004) to 50% in birch cuttings (Matyssek *et al.*, 1995).

Despite rather low levels of expected regional drought indicated for this region by the PDSI, the soils at Look Rock became very dry within a period of approx. 2 wk during high ozone exposures in late summer (Fig. 3). Canopy conductance and soil-moisture analyses suggested that ozone contributed to the rapid loss of water from the rooting zone of trees, and had exacerbated water stress at this site. Cell division and expansion are among the physiological processes most sensitive to water stress, and are affected at much lower stress levels than photosynthesis (Hsaio *et al.*, 1976). Thus water-stress effects under these conditions may be more important in limiting growth than reductions in photosynthetic production (Luxmoore *et al.*, 1997).

Water-stress effects can also be particularly significant in the forest understory (Orwig & Abrams, 1997; Hanson *et al.*, 2001), where vegetation is typically poorly adapted to such stresses. Increased water use of overstory trees, particularly episodic stresses such as we report here with elevated ozone levels, would probably be even more detrimental to understory vegetation. Symptoms of moisture stress were very apparent in understory vegetation at Look Rock by early August 2002, and included rapid mortality of some tree saplings and visual stress symptoms in several other understory plant species.

Our data suggest that ozone uptake by vegetation in our region will probably be increased both directly by higher ozone exposure, and indirectly in response to increased canopy conductance during higher-ozone episodes. Grulke *et al.* (2002b) have found that uptake of $O_3$ by ponderosa pine was very highly correlated ($R^2 = 0.92$) with stomatal conductance. In our studies, sap flow and associated canopy conductance appeared to be most affected by episodic exposure to high hourly $O_3$ levels. Peak hourly values during the day appeared to have the strongest influence on changes in water-use patterns, as shown by sensitivity analyses of responses of daily averaged canopy conductance to $O_3$ exposure over various averaging intervals. Thus we assume that ozone uptake is highest during and after the 3–5-d high-exposure episodes typical of this region. Such exposure episodes also appeared to play an important role in both episodic and seasonal responses in water use and growth of large trees (McLaughlin *et al.*, 2007). Significantly, daily averaged peak $O_3$ levels were also identified as most significant in affecting soil-moisture status in the rooting zone of sample trees, and in altering annual late-season baseflow of WBWS.

The episodic nature of ambient ozone exposures in the field suggests that threshold exposure levels derived from studies at

constant ozone levels may not reproduce some of the most biologically important features of exposure dose. Additional understanding of tree responses to short-term variations in exposure dose will probably be very important for determining critical ozone-exposure levels for trees under variable environmental regimes in the field. Our studies suggest that different indices of ozone exposure may be needed for different components of plant response (chronic loss in growth vs increased water stress) under field conditions.

## Implications for forest hydrologic processes

Streamflow analyses, initiated in response to apparent changes in forest water use, indicate that ozone can contribute significantly to reduced baseflows from forested catchments during low-flow periods in the fall. Rather large (> 25%) changes in forest cover have historically been considered necessary to affect baseflows (McGuinness & Harrold, 1971; Johnson, 1998), and this lack of sensitivity has been attributed in part to the masking effects of climatic variations (Robinson *et al.*, 2003). Our study indicates that ozone can be an important component of those climatic variations. Increasing forest water use with increasing ozone levels contributed significantly to reduced late-season baseflows in all three watersheds examined. Empirically based model simulations indicate that these effects can be large, and are statistically significant. Rather modest (25%) reductions in annual ozone-exposure levels are projected to increase baseflow significantly in late autumn (Fig. 4). It is important to note that the changes we have reported are probably most pronounced in the late-autumn measurement period, when the cumulative seasonal effects of changes in leaf physiological processes by ozone would be maximized. However, changes in baseflow of the magnitude found here during the critical low-flow period would be expected to have profound implications for water quality and stream ecology, particularly for the lower-order feeder streams. In these streams, such changes would affect nutrient and pollutant concentrations, water temperatures and concentrations of dissolved oxygen. All these factors are important to the survival and diversity of aquatic life in these small streams.

For both the exploratory initial model and the more advanced model based on daily analyses of streamflow for WBWS (Table S3), our regression analyses detected both dominant negative effects of $O_3$ (maximum hourly $O_3$ per day) and less significant positive effects (AOT60 or sumO60) on streamflow. The net effect of these two types of effect was consistently negative (Fig. 4); however, the model suggests that the relationship between $O_3$ exposure and late-season baseflow may have a nonlinear component, with streamflow occasionally being increased at the highest $O_3$ levels. Such a relationship is mechanistically plausible, as high ozone levels are known to both reduce canopy production and cause premature leaf fall (McLaughlin & Percy, 1999). Both responses would be expected to have a positive effect on baseflow in the highest-ozone years. This observation is supported by measurements of canopy-production data at WBWS (Hanson *et al.*, 2003), which documented reduced canopy production during 1998 and 1999, the years of highest ozone exposure in the entire data set. In addition, premature leaf senescence and leaf fall were noted in this region in connection with high $O_3$ levels in 2002. This indication of a potentially positive episodic effect of ozone on baseflow, observed at the relatively small, south-facing WBWS, was not observed with the lower $O_3$ levels in the large (12 500 ha) Cataloochie Creek watershed. There, only negative effects of $O_3$ on baseflow were detected.

We believe the analyses reported here should be extended to watersheds in other regions, and it is our plan to do so. Particularly important will be regions with lower ozone levels and/or different forest types. From a broader ecological perspective, the changes we have observed in this study should be considered in conjunction with reported reductions in soil organic matter (Loya *et al.*, 2003) and reduced root biomass in natural stands (Grulke *et al.*, 1998) observed under combinations of $O_3$ and other fossil fuel pollutants. Current estimates of ozone-induced reductions in carbon sequestration of 18–38 Tg C $yr^{-1}$ for North America are based on reductions in net primary production (Felzer *et al.*, 2004). Soil organic matter is a key factor in soil retention and supply of both water and nutrients (Reeves, 1997).

In conclusion, we believe that our results present a mechanistically plausible picture of the effects of ambient ozone and associated environmental variables on selected forest physiological and geophysical processes in this study region. Patterns of stem increment and water movement in forest trees, examined in relationship to a wide range of climatic variables, demonstrated that ambient ozone concentrations can significantly increase water use by forest trees. Peak hourly ozone exposure was found to increase canopy conductance of individual trees, and the effects of increased water uptake were reflected in reduced soil moisture in the rooting zone of sample trees. The significance of ozone stimulation of forest water use at the tree and soil level was supported by analysis of changes in baseflow of regional watersheds. The cumulative effects of daily peak ozone exposures were also shown to be relatively more important than longer-term averages in increased water use at both tree and watershed scales.

These studies indicate that ozone is an important component of the current climate, and that anthropogenic contributions of ozone will probably exacerbate the adverse effects of global warming by reducing the water available to support both forest and stream ecosystems. Changes in patterns of water use and retention by terrestrial systems can be expected to amplify the effects of drought, particularly late in the growing season when water use by vegetation most strongly influences baseflow of streams. The importance of forest growth and water use to forest ecosystem function, and the linkages of forests to aquatic and human ecology, suggest that ozone should be considered an important part and a potentially significant amplifier of the projected ecological effects of global warming.

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## Supplementary Material

The following supplementary material is available for this article online:

**Section S1** Expanded descriptions of sampling methodology and data sources

**Section S2** Three tables providing documentation of structure and performance of empirical models of canopy conductance, soil-moisture status and streamflow

**Section S3** Documentation of serial correlations for both dependent and representative independent variables considered in these studies. Pearson correlations relate each variable to its time-lagged value

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